PINE

Pleistocene Refugia for Longleaf and Loblolly Pines

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INTRODUCTION

Longleaf pine (*P. palustris* Mill.) and loblolly pine (*P. taeda* L.) are two species that are common to the coastal plain of the southeastern United States. The current natural range of the two species is largely overlapping. Loblolly pine occurs in 13 southeastern states (Figure 1). Longleaf pine is the more austral of the two species, occurring further south into peninsular Florida, but not occurring naturally in Oklahoma, Arkansas, Tennessee, Maryland and New Jersey (Critchfield and Little, 1966). The two species are closely related. They sometimes hybridize naturally (Chapman, 1922), and creating the artificial hybrid is not difficult if longleaf pine is the female parent (Snyder and Squillace, 1966).

Very little is known about the location of the southern pines during the Wisconsin glaciation because of the lack of macrofossils. Palyno-

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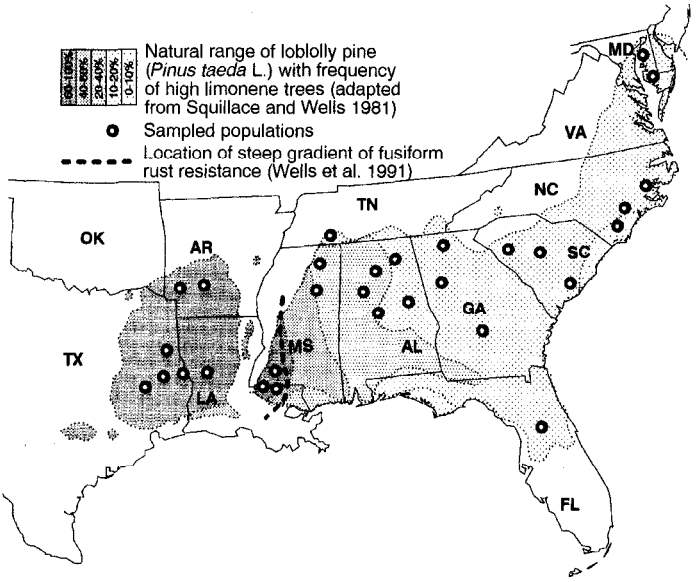
FIGURE 1. Natural range of loblolly pine showing proportion of trees with high concentrations of cortical limonene.



logical records are not conclusive, due to the difficulty in identifying pine pollen to the species level. Macrofossils of spruce (*Picea* sp.) dating from the Pleistocene have been found within the current range of both longleaf and loblolly pine in southern Louisiana, central Georgia and southern North Carolina, indicating that the climate was considerably colder at that time (Watts, 1983). It is reasonable to assume that longleaf and loblolly pine were situated south of their present range during the Pleistocene. The exact location of these refugia is a matter of some speculation (Wells et al., 1991), but considering the relatively uniform land form of the lower Coastal Plain of the southeastern United States, there appears to be only two possibilities; south Florida/Caribbean or south Texas/northeast Mexico.

Genetic data can be used to infer location of glacial refugia and migration patterns (Wheeler and Guries, 1982). The present study examines geographic patterns of allozyme variation in longleaf and loblolly pines to provide evidence for the location of Pleistocene refugia for the two species.

MATERIALS AND METHODS

Allozyme frequencies were studied in range-wide collections from 23 populations of longleaf pine (Schmidtling and Hipkins, 1998) and 33 populations of loblolly pine (Figure 1). The longleaf pine data were from megagametophytes of approximately 30 individual trees per population, and included three seed orchard sources and an old-growth stand. In loblolly pine, three different sets of range-wide collections were used; nine seed orchard populations averaging 46 clones per source, 14 populations from the Southwide Southern Pine Seed Source Study (Wells and Wakeley, 1966) averaging 46 megagametophytes per source, and 10 bulk seed collections, averaging 66 embryos per source.

In both species, gel electrophoresis was used to resolve enzyme systems phosphoglucose isomerase (PGI), fluorescent esterase (FEST), malic enzyme (ME), aconitase (ACO), phosphoglucomutase (PGM). 6-phosphogluconate dehydrogenase (6PGD), glutamic oxaloacetate transaminase (GOT), leucine aminopeptidase (LAP), isocitrate dehydrogenase (IDH), and malate dehydrogenase (MDH), for a total of 10 enzyme systems and 16 loci. In longleaf, an additional 4 enzyme systems and 6 loci were assayed; alcohol dehydrogenase (ADH), triosephosphate isomerase (TPI), glycerate-2-dehydrogenase (GLYDH), and glucose-6-phosphate dehydrogenase (G6PD).

Allozyme data were used to provide several estimates of genetic variation using BIOSYS I (Swofford and Selander, 1989), including mean number of alleles per polymorphic loci (N,), percent loci polymorphic (P_l, 95% criterion), observed heterozygosity (H,), and expected heterozygosity (H,), as well as the standard measures of genetic differentiation, the F statistics FIS, F_{IT} and F_{ST}.

Additional measures of diversity computed were (N,) number of rare alleles per tree (one that occurs at a frequency of 0.05 or less in the overall population) and the frequency of the most common allele (A,.) averaged over all loci. A "diversity index" was computed by taking the mean of the standardized scores for N_a, P_l, H_e, N_r, and A_c^{-1} for each population. Each measure of genetic diversity is first standardized by subtracting the mean and dividing by the standard deviation, and the "index" is the unweighted mean of the five scores.

RESULTS AND DISCUSSION

F statistics for both species indicated very little inbreeding with F_{IS} and F_{IT} near zero or slightly negative. F_{ST} was between 0.03 and 0.04, indicating that differences among populations accounted for between 3 and 4 percent of the total variation in both species. There was little difference in allele frequencies due to origin of the populations, i.e., orchard versus wild populations, for loblolly (Schmidtling et al., 1994) or longleaf (Schmidtling and Hipkins, 1998).

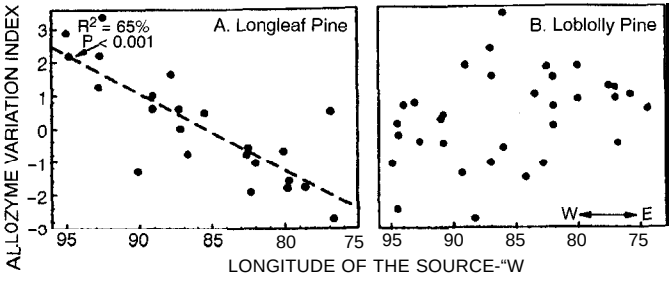
In longleaf pine, there was a linear decrease in allozyme variation from west to east. Correlations of longitude of the seed source with N_a, H_o, P_l, N_r, and A_c^{-1} were r = 0.604, 0.787, 0.718, 0.549 and 0.728, respectively, which are all significant at the 0.01 level. The best correlation was between longitude and the composite function, the allozyme variation index (Figure 2A).

In loblolly pine, there was no east-west trend in allozyme variation, and there appeared to be a tendency for more variation in the central part of the natural range (Figure 2B).

Provenance tests have shown that substantial geographic variation in growth, survival, and disease susceptibility exists in loblolly pine as well as in longleaf pine (Wells and Wakeley, 1966, 1970). Growth is generally related to latitude or temperature at the seed source (Schmidtling, 1997). Geographic variation in both species parallels that of other forest tree species; seed sources from warmer climates grow faster than those from colder climates, if these sources are not transferred to very different climates.

East-west variation in adaptive traits such as growth, disease re-

FIGURE 2. Plot of allozyme variation index vs. longitude of the seed source for range-wide collections of (A) longleaf pine and (B) loblolly pine.



sistance and survival is minimal in longleaf pine, but is quite important in loblolly pine (Wells and Wakeley, 1966, 1970). In loblolly pine, western sources are slower growing, survive better, have greater resistance to fusiform rust (*Cronartium quercuum* [Berk.] Miyabe ex Shirai f.sp. *fusiforme*), and have greater concentrations of limonene in cortical gum than eastern sources (Squillace and Wells 198 1, Figure 1). The isolating effect of the pineless Mississippi River Valley has been proposed as the reason for these differences (Wells and Wakeley, 1966), but if geographic variation in limonene concentration and fusiform rust resistance are considered (Figure 1) the division between western and eastern sources appears to be east of the Mississippi River.

CONCLUSIONS

It is proposed that the continuous linear decrease in allozyme variation in longleaf pine from west to east is a result of migration from a single refugium in the west (south Texas or northeast Mexico) after the Pleistocene, with a loss of variability due to stochastic events during migration. The lack of such a trend in allozymes in loblolly pine, coupled with the distinct east versus west variation in fusiform rust resistance and other adaptive traits suggest that loblolly pine was located in two refugia during the Pleistocene: in Texas/Mexico and Florida/Caribbean, as proposed by Wells et al. (1991).

The dashed line east of the Mississippi, in southeast Louisiana and west Mississippi (Figure 1) shows the location of a very steep gradient in fusiform rust resistance which can best be explained by assuming the confluence of two populations (Wells et al., 1991). This, as well as the steep gradient in terpene concentration in the same location suggests the merging and mixing of the two populations after the retreat of the Wisconsin glaciation.

Seed movement guidelines should take into account the differences among the two species. It does not appear that east-west movement of longleaf seed sources need be restricted, especially if seed of the more diverse western populations are moved eastward. More caution should be used in east-west movement of loblolly pine, since there appear to be two different populations.

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